Zoosyst. Evol. 100 (4) 2024, 1387–1400 | DOI 10.3897/zse.100.118522

PENSOFT

MUSEUM FÜR NATURKUNDE BERLIN

The ornate rubbernose pleco (Siluriformes, Loricariidae, *Chaetostoma*), a new species from the Ucayali River Basin, Peru

Vanessa Meza-Vargas[1,2], Jorge L. Ramirez[1,2], Nathan K. Lujan[3,4]

1 *Departamento de Ictiología, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Avenida Arenales 1256, Jesus Maria, Lima 14, Peru*

2 *Departamento de Biología Celular y Genética, Facultad de Ciencias Biológicas, Universidad Nacional Mayor de San Marcos, Avenida Germán Amézaga 375, Cercado De Lima, Lima, Peru*

3 *Department of Natural History, Royal Ontario Museum, 100 Queens Park, Toronto, ON M5S 2C6, Canada*

4 *Ecology and Evolutionary Biology Department, University of Toronto, 25 Willcocks St, Toronto, ON M5S 3B2, Canada*

https://zoobank.org/9D3FFC51-0277-4669-B215-23DA5A1D5483

Corresponding author: Vanessa Meza-Vargas (meza.sv@gmail.com)

Academic editor: Nicolas Hubert ♦ **Received** 11 January 2024 ♦ **Accepted** 14 August 2024 ♦ **Published** 18 October 2024

Abstract

A new species in the rubbernose catfish genus *Chaetostoma* is described from the Aguaytia, Pisqui and Palcazu Rivers, which drain the Pampa de Sacramento Region in the Ucayali River drainage of central Peru. The new species is distinguished from congeners, except *C. anomalum*, *C. branickii*, *C. dorsale*, *C. leucomelas*, *C. microps*, *C. nudirostre*, *C. palmeri* and *C. thomsoni* by having distinct, white, variably-shaped spots or vermiculations ½–2× nostril diameter on dark grey to black background on the head (vs. spots absent or black on light-coloured background). The new species is distinguished from *C. anomalum*, *C. branickii*, *C. dorsale*, *C. microps*, *C. nudirostre* and *C. thomsoni* by having highly variable, distinct white spots, vermiculations or bands ½–10× nostril diameter on the body, from *C. leucomelas* by having dorsal and caudal fin indistinctly and variably-patterned with zero to four bands (vs. dorsal and caudal fin consistently having five or more uniform bands) and from *C. palmeri* by having two predorsal plates (vs. three), supraoccipital excrescence present (vs. absent) and pelvic-fin insertion slightly posterior to dorsal-fin insertion (vs. pelvic-fin insertion at middle of dorsal-fin base). Species delimitation analyses of the COI and Cytb genes further support the recognition of this new species.

Key Words

Amazon, Andes, Chaetostoma clade, freshwater, molecular, Neotropical, taxonomy

Introduction

With over 1060 currently valid species, 19% of which (200) were described in the last decade, the suckermouth armoured catfish family Loricariidae is the fifth largest vertebrate family and one of the fastest growing (Fricke et al. 2024). Of the four vertebrate families that are more species-rich (Characidae, Cichlidae, Cyprinidae and Gobiidae), none is growing as quickly or is as geographically restricted as Loricariidae, which naturally occurs only in fresh or estuarine waters from southern Costa Rica to northern Argentina. Within Loricariidae, the rubbernose catfish genus *Chaetostoma* Tschudi 1846 is the third most species-rich genus with 49 valid species (Meza-Vargas et al. 2022), being superseded only by *Hypostomus* (> 150 valid species) and *Ancistrus* (76 valid species) (de Queiroz et al. 2020; Neuhaus et al. 2023). *Chaetostoma* is also the most geographically restricted of these species-rich genera, with 46 species being restricted to flanks of the Andes and Caribbean Coastal mountains from Panama to southern Peru and three species (*C. jegui*, *C. orientale* and *C. vasquezi*) occurring in rivers draining the Guiana or Brazilian shields (Meza-Vargas et al. 2022).

All but one species of *Chaetostoma* (*C. platyrhynchus*) are externally distinguished from most other loricariid genera by having the anterior and anterolateral snout

Copyright *Meza-Vargas, V. et al.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

margins free of plates, with this region instead being covered by a broad band of naked (i.e. unplated) skin, lacking tentacles. Five other loricariid genera also have unplated snout margins (*Ancistrus* Kner, 1854, *Corumbataia* (Britski, 1997), *Paulasquama* Armbruster & Taphorn, 2011, *Soromonichthys* Lujan & Armbruster, 2011 and *Transancistrus* Lujan, Meza-Vargas & Barriga-Salazar, 2015), but only *Ancistrus* and *Transancistrus* are sympatric with *Chaetostoma*. *Chaetostoma* can be easily distinguished from *Ancistrus* by lacking snout tentacles (vs. tentacles present), having at least five longitudinal series of plates at the shallowest part of the caudal peduncle (vs. three) and having eight or more branched dorsal-fin rays (vs. seven). The only *Chaetostoma* with a fully-plated snout (*C. platyrhynchus*) is restricted to the upper Caqueta and Napo drainages of Colombia and Ecuador, respectively; it shares all other traits above with congeners.

Chaetostoma has never undergone a comprehensive species-level taxonomic revision, though Lujan et al. (2015b) reviewed species from the centre of the genus's geographic range in and around Ecuador and provided a multi-locus molecular phylogenetic hypothesis spanning many species and the entire geographic range of the genus. This analysis was recently enlarged and updated by Meza-Vargas et al. (2022). Both studies used combinations of up to 18 external morphological traits including colouration, meristics and morphometrics to distinguish amongst 13 species from rivers draining east of the Andes (cis-Andean), making taxonomy of the cis-Andean distribution of *Chaetostoma* the most well-studied (Salcedo 2006a, 2006b; Salcedo and Ortega 2015; Ballen et al. 2016). Within this distribution, the Huallaga River in central Peru is the epicentre of species diversity, with seven species currently recognised: *C. changae*, *C. daidalmatos*, *C. lexa*, *C. marmorescens*, *C. stroumpoulos*, *C. taczanowskii*, and *C. trimaculineum*. In the much larger Ucayali River drainage, which borders the Huallaga to the east and south, only two species are currently known: *C. lineopunctatum* and *C. loborhynchos*. In this paper, we describe a new, third species for the Ucayali River drainage. Seidel (2011) first reported this species as undescribed in the ornamental aquarium fish literature, simultaneously highlighting the species' considerable colour pattern variation by assigning it three different L-numbers (L455, L456, L457). L-numbers are codes used by the ornamental aquarium fish industry to differentiate amongst and market distinct, often scientifically undescribed colour morphs (Stawikowski 1988).

In scientific literature, the species was first recognised as new by Lujan et al. (2015a), who referred to it as '*Chaetostoma* n.sp. Ucayali' and included it in a multi-locus molecular phylogenetic analysis. This analysis found the new species to be part of a polytomy containing *C. breve*, *C. dermorhynchus*, *C. dorsale*, *C. formosae*, *C. orientale* (then *Chaetostoma* n.sp. Xingu), *C. trimaculineum* and an undescribed species from the Orinoco River Basin. In a re-analysis and expansion of the Lujan et al. (2015c) dataset, Meza-Vargas et al. (2022) found the new species to be sister to *Chaetostoma breve* Regan, 1904, a species whose nomenclature we revisit in light of these phylogenetic results and a large series of more recently collected topotype material for *Chaetostoma branickii* Steindachner, 1881.

Material and methods

Taxon sampling

This study is based mostly on 12 formalin-fixed, 70% ethanol-preserved, museum-catalogued specimens of the undescribed species collected from the Aguaytia River and the Raya and Omaiz Rivers in the Palcazu River drainage (Fig. 1) in August and September 2022 and on 313 specimens of *Chaetostoma branickii* collected in the Marañon River drainage in August 2018 (collection permit: N° 00680-2022-PRODUCE/DGPCHDI). Specimens were euthanised prior to preservation by overdose of eugenol (clove oil) until ventilation stopped for at least 30 minutes in adherence with an institutional animal use protocol approved by Auburn University (protocol 2018–3354; Lucena et al. (2013)). Institutional codes follow Sabaj (2020).

Gene amplification and sequencing

Genetic samples of fin or muscle tissue were dissected prior to specimen fixation and individually linked to source specimens using unique, matching alphanumeric tags on voucher specimens and cryosafe tubes, then preserved in 95% ethanol. Whole genomic DNA was extracted from tissue subsamples using a salt precipitation protocol (Alijanabi and Martinez 1997). DNA sequence data were obtained for two mitochondrial markers: Cytochrome C oxidase I (COI) and Cytochrome b (CytB). A 658-base region of COI was amplified using the primers ANOSCOIF and ANOSCOIR (Ramirez and Galetti 2015) and a 1150-base region of the mitochondrial CytB gene was amplified using the primers and protocol of Lujan et al. (2015a). Amplified gene regions were sequenced on an ABI 3730 capillary sequencer at the Royal Ontario Museum (Toronto, Canada) or sent for sequencing at Macrogen Inc. (Seoul, South Korea).

Molecular analyses

Sequences for each gene were automatically aligned using Clustal W (Larkin et al. 2007) then manually edited and checked to ensure the absence of internal stop codons. *De novo* CytB sequences were compared with existing data for the *Chaetostoma* Clade from Lujan et al. (2015b) and additional COI sequences were obtained from BOLD (Table 1). Both gene datasets were used to run three species delimitation methods: the General Mixed Yule Co-

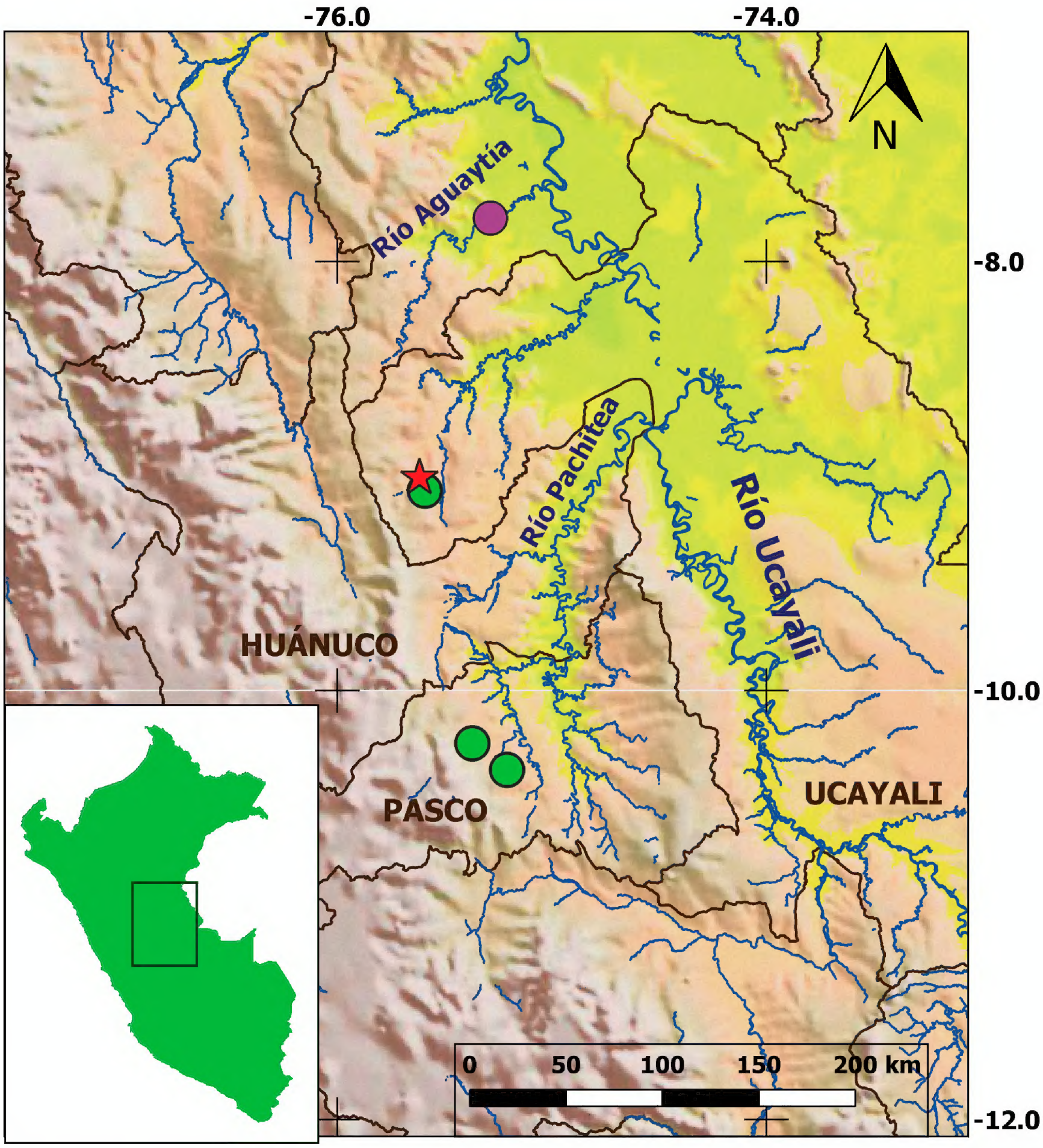

Figure 1. Distribution of *Chaetostoma sacramento* type specimen sample sites along the Pampa del Sacramento in Andean left-bank tributaries of the Ucayali River Basin. Holotype (red star), green dots (paratypes), purple dots (aquarist trade).

alescent model (GMYC) with a single threshold (Pons et al. 2006), the Bayesian implementation of the PTP model (bPTP) (Zhang et al. 2013) and the Assemble Species by Automating Partitioning (ASAP) method (Puillandre et al. 2021). As input for the first two methods, an ultrametric tree was built using BEAST v.2.7.4 (Bouckaert et al. 2014) with a GTR+I molecular evolution model for COI and an HKY+I+G model for CytB, a fast log-normal relaxed clock and a birth-death tree model. The analyses were run for 100 million Markov Chain Monte Carlo (MCMC) generations with the first 10% discarded as burn-in. Convergence of MCMC chains within a stable range and effective sample sizes (ESS) greater than 200 were confirmed in Tracer v.1.6 (Rambaut et al. 2014). The pipeline SPdel (Ramirez et al. 2023) was used to compute and compare all delimitation methods.

Morphological analysis

Morphometric landmarks follow Armbruster (2003) with lateral trunk plate row terminology following Schaefer (1997) and cheek odontode type following Lujan et al. (2015b). Standard length (SL) is expressed in mm and other measurements are expressed as percentages of either standard length or, for subunits of the head, head length. Measurements and counts were taken on the left side of specimens when possible.

Table 1. Tissue samples used in the molecular species delimitation analyses, including GenBank accession number (coI = Cytochrome oxidase subunit I, cytb = cytochrome b), voucher specimen catalogue number, country and drainages of origin. Bold accession numbers = new sequences for this study.

Taxa	Tissues Number	cytb	col	Catalogue Number	Country	Drainage
Chaetostoma anale	T24822	OL303592	–	ROM 107267	Colombia	Orteguasa
Chaetostoma anale	T24946	OL303593	OK514631	ROM 107837	Colombia	Orteguasa
Chaetostoma anale	T24906	OL303604	OK514628	ROM 107811	Colombia	Caqueta
Chaetostoma anale	T24907	OL303605	OK514629	ROM 107811	Colombia	Caqueta
Chaetostoma anomalum	T631	OL303608	–	INHS 55455	Venezuela	Maracaibo
Chaetostoma bifurcum	T13602	KP960196	–	ROM 93687	Ecuador	Esmeraldas
Chaetostoma bifurcum	T13603	OL303609	–	ROM 93687	Ecuador	Esmeraldas
Chaetostoma bifurcum	T13665	OL303610	–	ROM 93721	Ecuador	Guayas
Chaetostoma bifurcum	T13896	OL303611	–	ROM 93787	Ecuador	Santa Rosa
Chaetostoma bifurcum	T13897	OL303612	–	ROM 93787	Ecuador	Santa Rosa
Chaetostoma breve	P6292	KP960190	–	AUM 46515	Peru	Marañon
Chaetostoma breve	PE08208	OL303613	–	MHNG 2712.047	Peru	Huallaga
Chaetostoma breve	PE08213	OL303614	–	MHNG 2712.048	Peru	Huallaga
Chaetostoma breve	PE08648	OL303615	–	MHNG 2712.074	Peru	Huallaga
Chaetostoma breve	PE08673	OL303616	–	MHNG 2712.078	Peru	Huallaga
Chaetostoma breve	P6294	OL303617	–	AUM 46516	Peru	Marañon
Chaetostoma breve	T14360	OL303618	–	ROM 93950	Ecuador	Napo S
Chaetostoma breve	T19715	OL303619	–	ROM 100323	Ecuador	Napo N
Chaetostoma breve	T19716	OL303620	–	ROM 100320	Ecuador	Napo N
Chaetostoma breve	T14224	OL303621	–	ROM 93923	Ecuador	Pastaza
Chaetostoma breve	T14005	OL303622	–	ROM 93848	Ecuador	Santiago
Chaetostoma brevilabiatum	6630	OL303623	–	ANSP 189597	Colombia	Honda
Chaetostoma brevilabiatum	6631	OL303624	–	ANSP 189597	Colombia	Honda
Chaetostoma cf. *anale*	T19707	OL303594	–	ROM 100322	Ecuador	Napo
Chaetostoma cf. *anale*	T19708	OL303595	OK514634	ROM 100322	Ecuador	Napo
Chaetostoma cf. *anale*	T19606	OL303628	OK514632	ROM 100250	Ecuador	Napo
Chaetostoma cf. *anale*	T19647	OL303629	–	ROM 100263	Ecuador	Napo
Chaetostoma cf. *fischeri*	T9034	KP960197	–	STRI 11581	Panama	Tuira
Chaetostoma cf. *lineopunctatum*	CH153	OL303630	–	MUSM 44253	Peru	Huallaga
Chaetostoma cf. *lineopunctatum*	PE08318	OL303631	–	MHNG 2712.057	Peru	Huallaga
Chaetostoma cf. *lineopunctatum*	PE08545	OL303632	–	MHNG 2712.069	Peru	Huallaga
Chaetostoma cf. *loborhynchus*	CH200	OL303633	–	MUSM 44899	Peru	Huallaga
Chaetostoma cf. *loborhynchus*	CH202	OL303634	–	MUSM 44899	Peru	Huallaga
Chaetostoma cf. *loborhynchus*	CH2023	OL303635	–	MUSM 44899	Peru	Huallaga
Chaetostoma cf. *loborhynchus*	CH204	OL303636	–	MUSM 44899	Peru	Huallaga
Chaetostoma changae	PE08442	OL303637	–	MHNG 2712.064	Peru	Huallaga
Chaetostoma changae	PE08543	OL303638	–	MHNG 2712.067	Peru	Huallaga
Chaetostoma chimu	TICT-FCA-07	–	FBCH009-21	–	Colombia	Meta
Chaetostoma chimu	TICT-FCA-223	–	FBCH118-21	–	Colombia	Meta
Chaetostoma chimu	TICT-FCA-148	–	FBCH143-21	–	Colombia	Meta
Chaetostoma daidalmatos	CH140	OL303639	–	MUSM 44845	Peru	Huallaga
Chaetostoma daidalmatos	CH141	OL303640	–	MUSM 44845	Peru	Huallaga
Chaetostoma daidalmatos	PE08191	OL303641	–	MHNG 2712.045	Peru	Huallaga
Chaetostoma daidalmatos	PE08207	OL303642	–	MHNG 2712.051	Peru	Huallaga
Chaetostoma daidalmatos	PE08347	OL303644	–	MHNG 2712.055	Peru	Huallaga
Chaetostoma dermorhynchus	T14258	KP960191	–	ROM 93656	Ecuador	Pastaza
Chaetostoma dermorhynchus	T14287	OL303647	–	ROM 93656	Ecuador	Pastaza
Chaetostoma dermorhynchus	T14293	OL303648	–	ROM 93946	Ecuador	Bobonaza
Chaetostoma dermorhynchus	T14296	OL303649	–	ROM 93946	Ecuador	Bobonaza
Chaetostoma dermorhynchus	T14308	OL303650	–	ROM 93946	Ecuador	Bobonaza
Chaetostoma dorsale	TICT-FCA-08	–	FBCH008-21	–	Colombia	Meta
Chaetostoma dorsale	TICT-FCA-168	–	FBCH078-21	–	Colombia	Meta
Chaetostoma dorsale	TICT-FCA-185	–	FBCH086-21	–	Colombia	Meta
Chaetostoma dorsale	TICT-FCA-244	–	FBCH091-21	–	Colombia	Meta
Chaetostoma fischeri	T9026	KP960195	–	STRI 7604	Panama	Chagres
Chaetostoma fischeri	T9027	OL303651	–	STRI 905	Panama	Bayano

Taxa	Tissues Number	cytb	col	Catalogue Number	Country	Drainage
Chaetostoma fischeri	T9036	OL303652	–	STRI 12274	Panama	Bayano
Chaetostoma fischeri	T9037	OL303653	–	STRI	Panama	Chagres
Chaetostoma fischeri	STRI-01740	–	BSFFA489-07	–	Panama	Tuira
Chaetostoma fischeri	STRI-01732	–	BSFFA490-07	–	Panama	Acla
Chaetostoma fischeri	STRI-01735	–	BSFFA491-07	–	Panama	Bayano
Chaetostoma fischeri	STRI-01754	–	BSFFA492-07	–	Panama	Tuira
Chaetostoma fischeri	STRI-01760	–	BSFFA493-07	–	Panama	Bayano
Chaetostoma fischeri	STRI-07104	–	BSFFA735-07	–	Panama	Chagres
Chaetostoma formosae	T17431	OL303654	–	ROM 95260	Colombia	Meta
Chaetostoma formosae	TICT-FCA-64	–	FBCH052-21	–	Colombia	Meta
Chaetostoma guairense	VZ122	OL303655	–	INHS 34786	Venezuela	Limon
Chaetostoma jegui	Tec63785	OL303596	OK514635	LBP 15478	Brazil	Branco
Chaetostoma jegui	Tec63786	OL303597	OK514636	LBP 15478	Brazil	Branco
Chaetostoma joropo	T17428	OL303656	–	ROM 95259	Colombia	Meta
Chaetostoma joropo	T17429	OL303657	–	ROM 95259	Colombia	Meta
Chaetostoma joropo	TICT-FCA-208	–	FBCH134-21	–	Colombia	Meta
Chaetostoma joropo	TICT-FCA-224	–	FBCH136-21	–	Colombia	Meta
Chaetostoma joropo	TICT-FCA-245	–	FBCH137-21	–	Colombia	Meta
Chaetostoma leucomelas	–	–	CIUA550-20	–	Colombia	Cauca
Chaetostoma leucomelas	–	–	CIUA557-20	–	Colombia	Cauca
Chaetostoma leucomelas	CIUA-7439	–	UDEA074-18	–	Colombia	Cauca
Chaetostoma leucomelas	CIUA-7441	–	UDEA075-18	–	Colombia	Cauca
Chaetostoma leucomelas	CIUA-7482	–	UDEA076-18	–	Colombia	Magdalena
Chaetostoma leucomelas	CIUA-7491	–	UDEA077-18	–	Colombia	Magdalena
Chaetostoma lineopunctatum	P4772	GU569899	EU359409	ANSP 180446	Peru	Urubamba
Chaetostoma lineopunctatum	P4814	GU569913	EU359410	ANSP 180448	Peru	Madre de Dios
Chaetostoma lineopunctatum	PE08047	KP960199	–	MHNG 2712.041	Peru	Ucayali
Chaetostoma lineopunctatum	T10088	OL303658	–	AUM 51166	Peru	Madre de Dios
Chaetostoma lineopunctatum	T10089	OL303659	–	AUM 51166	Peru	Madre de Dios
Chaetostoma loborhynchos	TK70561	KJ947862	–	MUSM 20291	Peru	Tulumayo
Chaetostoma loborhynchos	TK70563	KJ947864	–	MUSM 20291	Peru	Tulumayo
Chaetostoma loborhynchos	TK70579	KJ947865	–	MUSM 20307	Peru	Paucartambo
Chaetostoma loborhynchos	TK70580	KJ947866	–	MUSM 20307	Peru	Paucartambo
Chaetostoma loborhynchos	TK70581	KJ947867	–	MUSM 20307	Peru	Paucartambo
Chaetostoma marmorescens	CH198	KP960194	–	MUSM 44898	Peru	Huallaga
Chaetostoma marmorescens	CH197	OL303660	–	MUSM 44898	Peru	Huallaga
Chaetostoma marmorescens	CH199	OL303661	–	MUSM 44898	Peru	Huallaga
Chaetostoma microps	T14125	KP960189	–	ROM 93895	Ecuador	Santiago
Chaetostoma microps	CH121	OL303662	–	MUSM 44313	Peru	Huallaga
Chaetostoma microps	CH149	OL303665	–	MUSM 44869	Peru	Huallaga
Chaetostoma microps	CH150	OL303666	–	MUSM 44869	Peru	Huallaga
Chaetostoma microps	PE08190	OL303667	–	MHNG 2712.046	Peru	Huallaga
Chaetostoma microps	PE08580	OL303668	–	MHNG 2712.07	Peru	Huallaga
Chaetostoma microps	P6034	OL303669	–	AUM 45518	Peru	Marañon
Chaetostoma microps	T14364	OL303670	–	ROM 93949	Ecuador	Napo S
Chaetostoma microps	MEPN1255	OL303671	–	MEPN 1255	Ecuador	Napo S cave
Chaetostoma microps	MEPN1259	OL303672	–	MEPN 19165	Ecuador	Napo S cave
Chaetostoma microps	ROM 93902	OL303673	–	ROM 93902	Ecuador	Santiago
Chaetostoma microps	T14096	OL303674	–	ROM 93877	Ecuador	Yungantza
Chaetostoma microps	T14097	OL303675	–	ROM 93877	Ecuador	Yungantza
Chaetostoma milesi	JAM1984	OL303677	–	MPUJ	Colombia	Suaza
Chaetostoma milesi	CIUA-8907	–	UDEA079-18	–	Colombia	Magdalena
Chaetostoma milesi	T24605	OL303676	–	ROM 106963	Colombia	Suaza
Chaetostoma milesi	–	–	CIUA680-20	–	Colombia	Magdalena
Chaetostoma nudirostre	T2084	OL303682	–	ANSP 191471	Venezuela	Valencia
Chaetostoma orientale	B1464	OL303679	OK514638	ANSP 199686	Brazil	Xingu
Chaetostoma orientale	B1472	OL303680	OK514639	ANSP 199686	Brazil	Xingu
Chaetostoma orientale	B1487	OL303681	OK514640	ANSP 199686	Brazil	Xingu
Chaetostoma orientale	2606	–	OK514647	INPA-ICT 58146	Brazil	Xingu
Chaetostoma sacramento sp. nov.	PE08121	OL303678	–	MHNG 2712.042	Peru	Ucayali

Taxa	Tissues Number	cytb	col	Catalogue Number	Country	Drainage
Chaetostoma sacramento sp. nov.	LGBBF358	OR875871	OR859576	MUSM 72046	Peru	Ucayali
Chaetostoma sacramento sp. nov.	LGBBF359	OR875872	OR859577	MUSM 72046	Peru	Ucayali
Chaetostoma sacramento sp. nov.	MUSMT1564	–	OR859578	MUSM 71392	Peru	Ucayali
Chaetostoma sacramento sp. nov.	MUSMT1566	–	OR859579	MUSM 71392	Peru	Ucayali
Chaetostoma sp. Apure	T08954	OL303683	–	AUM 54034	Venezuela	Apure
Chaetostoma sp. Apure	T08955	OL303684	–	AUM 54034	Venezuela	Apure
Chaetostoma sp. Apure	T491	OL303685	–	AUM 41073	Venezuela	Apure
Chaetostoma sp. Apure	T621	OL303686	–	INHS 56147	Venezuela	Apure
Chaetostoma sp. CuruaUna	525	OL303599	OK514641	MCP 53005	Brazil	Curua-Una
Chaetostoma sp. L445	T12930	KP960193	–	ROM 94925	Colombia	Meta
Chaetostoma sp. L445	T17424	OL303687	–	ROM 95257	Colombia	Meta
Chaetostoma sp. L445	T17425	OL303688	–	ROM 95257	Colombia	Meta
Chaetostoma sp. Meta	–	–	CIUA698-20	–	Colombia	Cauca
Chaetostoma sp. Meta	–	–	CIUA707-20	–	Colombia	Cauca
Chaetostoma stroumpoulos	CH120	OL303689	–	MUSM 44303	Peru	Huallaga
Chaetostoma stroumpoulos	CH142	OL303691	–	MUSM 44847	Peru	Huallaga
Chaetostoma stroumpoulos	PE08210	OL303693	–	MHNG 2712.049	Peru	Huallaga
Chaetostoma thomsoni	JAM1966	OL303695	–	ICNMHN 17768	Colombia	Chucuri
Chaetostoma thomsoni	–	–	CIUA541-20	–	Colombia	Cauca
Chaetostoma thomsoni	–	–	CIUA542-20	–	Colombia	Cauca
Chaetostoma thomsoni	–	–	CIUA543-20	–	Colombia	Cauca
Chaetostoma thomsoni	–	–	CIUA544-20	–	Colombia	Cauca
Chaetostoma thomsoni	–	–	CIUA545-20	–	Colombia	Cauca
Chaetostoma thomsoni	–	–	CIUA546-20	–	Colombia	Cauca
Chaetostoma thomsoni	–	–	CIUA547-20	–	Colombia	Cauca
Chaetostoma thomsoni	–	–	CIUA553-20	–	Colombia	Cauca
Chaetostoma thomsoni	–	–	CIUA554-20	–	Colombia	Magdalena
Chaetostoma thomsoni	–	–	CIUA559-20	–	Colombia	Cauca
Chaetostoma thomsoni	–	–	CIUA560-20	–	Colombia	Cauca
Chaetostoma thomsoni	–	–	CIUA563-20	–	Colombia	Cauca
Chaetostoma thomsoni	–	–	CIUA565-20	–	Colombia	Cauca
Chaetostoma thomsoni	–	–	CIUA566-20	–	Colombia	Magdalena
Chaetostoma thomsoni	–	–	CIUA570-20	–	Colombia	Cauca
Chaetostoma thomsoni	–	–	CIUA572-20	–	Colombia	Cauca
Chaetostoma thomsoni	–	–	CIUA574-20	–	Colombia	Cauca
Chaetostoma thomsoni	–	–	CIUA576-20	–	Colombia	Cauca
Chaetostoma thomsoni	–	–	CIUA579-20	–	Colombia	Cauca
Chaetostoma thomsoni	–	–	CIUA580-20	–	Colombia	Cauca
Chaetostoma thomsoni	–	–	UDEA080-18	–	Colombia	Cauca
Chaetostoma thomsoni	–	–	UDEA083-18	–	Colombia	Cauca
Chaetostoma thomsoni	–	–	UDEA085-18	–	Colombia	Cauca
Chaetostoma trimaculineum	P6047	OL303696	–	AUM 45524	Peru	Marañon
Chaetostoma trimaculineum	T14136	OL303697	–	ROM 93894	Ecuador	Santiago
Chaetostoma vasquezi	T09945	KP960192	–	AUM 53812	Venezuela	Caura
Chaetostoma vasquezi	V27	OL303698	OK514643	AUM 36555	Venezuela	Caroni
Chaetostoma vasquezi	V28	OL303699	OK514644	AUM 36555	Venezuela	Caroni

Results

Taxonomic accounts

Chaetostoma sacramento sp. nov.

https://zoobank.org/5B9D5C88-4581-4EE0-A529-DABC39FFB914

Fig. 2, Tables 2, 3

Chaetostoma sp. nov. Ucayali: Lujan et al. (2015b) [molecular phylogeny].

Type material. ***Holotype*** • Adult MUSM 72045; 65.1 mm SL; Peru, Ucayali Department, Padre Abad Province, Boqueron District, Shambillo, Amazon Basin, Ucayali River, unnamed left-bank tributary of Aguaytia River; 09°0'29.88"S, 75°37'1.92"W; alt. 365 m; 07 Aug 2022; D. Faustino, J. Chuctaya, C. Nolasco, O. Quispe.

***Paratype*:** All Peru, Amazon – Ucayali River Basin • MHNG 2712.042, 1; 32.2 mm SL; tissues PE08-122, 123, 124; Padre Abad Province, Aguaytia River at mouth of the Boca Yurac River; 11 September 2008; S. Fisch- Muller, R. Covain, P. de Rham, H. Ortega, J. Figuerosa Minaya, J. Sanchez Ramirez • MUSM 71392, 4; 50.5–79.4 mm SL; Pasco Department, Oxapampa Province, Palcazu District, Raya River; 10°22'13.61"S, 75°7'52.90"W;

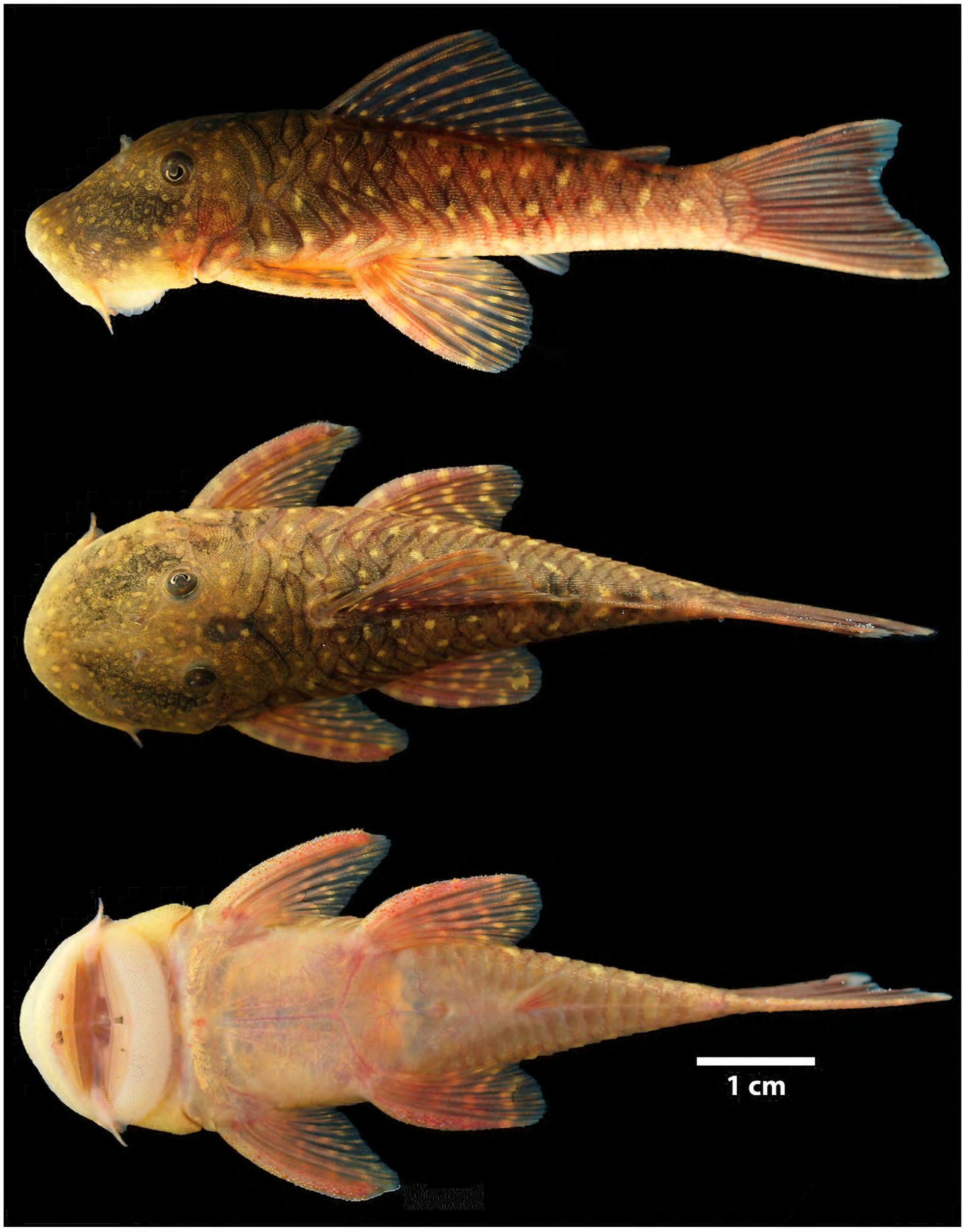

Figure 2. Live holotype of *Chaetostoma sacramento* MUSM 72045, 65.1 cm, collected from the Yamino River, a tributary of the Aguaytía River. Photos by D. Faustino.

7 September 2022; R. Olivera, R. Quispe, J. Arana, M. Paniagua • MUSM 72046, 34; 44.2–12.5 mm SL; Ucayali Department, Padre Abad Province, Padre Abad District, Aguaytia River; 9°4'8.58"S, 75°30'51.48"W; 8 August 2022; D. Faustino, J. Chuctaya, C. Nolasco, R. Quispe • ANSP 182805, 3; 57.8–70.5 mm SL; same data as MUSM 71392 • ROM 114668, 4; 54.3–76.7 mm SL; same data as MUSM 71392.

Genseq-2 COI. GenBank accession number. Obtained from paratypes MUSM 72046 (OR859576 and OR859577) and MUSM 71392 (OR859578 and OR859579).

Genseq-2 CytB. GenBank accession number. Obtained from paratypes MUSM 72046 (OR875871 and OR875872).

Diagnosis. *Chaetostoma sacramento* can be diagnosed from all congeners, except *C. anomalum*, *C. branickii*, *C. dorsale*, *C. leucomelas*, *C. microps*, *C. nudirostre*, *C. palmeri* and *C. thomsoni* by having distinct, white, variably-shaped spots or vermiculations ½–2× nostril diameter on grey to brown background on the head (vs. spots absent or black on light-coloured background). *Chaetostoma sacramento* is distinguished from *C. anomalum*, *C. branickii*, *C. dorsale*, *C. nudirostre* and *C. thomsonii* by having highly variable, small to large distinct white spots, vermiculations or bands on the body (vs. spots, vermiculations or bands absent or black on light-coloured background), from *C. anomalum* by having adipose fin fully formed (vs. rudimentary), from *C. dorsale* by having uniformly brown adipose fin (vs. adipose fin with black spot), from *C. leucomelas* by having golden spots across the dorsal fin rays (vs. light bands), from *C. microps* by having eight branched dorsal-fin rays (vs. nine), from *C. nudirostre* by having curved cheek odontodes (vs. strait), from *C. palmeri* by having two predorsal plates (vs. three), excrescence present (vs. absent) and pelvic-fin insertion slightly posterior of dorsal-fin insertion (vs. pelvic-fin insertion at middle of dorsal-fin base).

Description. Morphometric data in Table 2 and meristic data in Table 3. Snout moderately depressed, dorsal profile of head convex from snout tip to dorsal-fin origin, then straight and gradually descending to adipose fin. Caudal peduncle dorsal profile slightly concave. Ventral profile straight from snout to caudal fin. Body depressed, deepest at dorsal-fin origin, shallowest at caudal peduncle; greatest width at pectoral girdle. Caudal peduncle slightly compressed, roundly triangular in cross-section.

Head wide, anteriorly rounded in dorsal view; snout anterior margin unplated, lacking odontodes and tentacles. Orbit small (5.2–6.6% HL), dorsolaterally positioned, posterior margin aligned with vertical through anterior margin of cleithrum; skull roof flat. Oral disc wide, elliptical, occupying most of head width, lower lip ending just anterior to origin of opercular opening. Oval papillae covering upper lip, roundish papillae covering lower lip; all papillae smaller towards outer lip margins; lower lip margin crenulate. Buccal cavity with digitate papillae present posterior to premaxillary symphysis, one large patch of rugose papillae dorsomedial to each dentary tooth row. Maxillary barbel short (2.5–4.4% HL). Premaxillary tooth row straight, joining contralateral tooth row at 160° angle. Dentary straight, joining contralateral tooth row at 170° angle. Teeth small, villiform, asymmetrically bicuspid. Opercle external border having row of six straight odontodes, odontodes slightly larger than elsewhere on body. Three to five type 3 hypertrophied hook-like evertible cheek odontodes (mode 5), odontodes hooked anteriorly, not reaching cleithrum. Supraoccipital excrescence restricted to vestigial longitudinal unplated patch, keel absent.

Table 2. Morphometrics of *Chaetostoma sacramento*. Morphometric values as percentages of standard length (SL) or head length (HL). H = holotype, SD = standard deviation, (n = 11).

	H	Min	Max	Mean	SD
Standard length (mm)	65.13	50.49	76.74	63.7	–
Percent of standard length					
Head length	33.9	34.6	37.6	36.0	1.0
Predorsal length	43.4	41.9	47.3	45.1	1.5
Head-dorsal length	9.8	8.7	11.1	9.9	0.7
Cleithral width	33.6	29.3	33.4	32.0	1.2
Cleithral widest distance	37.1	34.8	36.5	35.7	0.5
Head-pectoral length	31.2	30.1	34.3	31.8	1.3
Thorax length	21.7	19.2	23.9	21.3	1.2
Pectoral-spine length	36.3	26.2	29.1	28.1	0.9
Abdominal length	25.4	23.0	25.5	24.5	0.7
Pelvic-spine length	25.7	24.8	28.5	26.4	1.0
Postanal length	30.2	29.1	34.8	32.0	1.4
Anal-fin spine length	15.0	8.7	10.4	9.8	0.5
Dorsal-pectoral distance	27.9	28.5	31.0	29.8	0.7
Dorsal spine length	26.7	25.5	29.4	27.8	1.0
Dorsal-pelvic distance	24.0	21.5	24.1	23.1	0.7
Dorsal-fin base length	28.7	25.0	26.4	25.5	0.4
Dorsal-fin base length	26.2	22.8	26.3	23.8	0.9
Dorsal-adipose distance	16.1	13.2	15.6	14.4	0.8
Adipose-spine length	8.2	7.7	9.4	8.2	0.5
Adipose-up. caudal distance	12.2	12.2	17.4	15.1	1.6
Caudal peduncle depth	15.2	12.4	13.9	13.1	0.6
Adipose-low. caudal distance	21.3	21.2	24.8	23.3	1.2
Adipose-anal distance	20.9	18.6	22.4	20.7	1.0
Dorsal-anal distance	17.1	15.6	17.0	16.3	0.5
Pelvic-dorsal distance	28.9	26.9	29.7	27.9	0.9
Percent of head length					
Head-eye length	29.7	10.0	11.1	10.6	0.3
Orbit diameter	14.0	5.2	6.6	5.9	0.4
Snout length	71.4	22.7	24.9	23.6	0.7
Internares width	14.5	4.6	5.7	5.2	0.4
Interorbital width	45.0	13.8	16.1	15.1	0.7
Head depth	71.9	24.7	26.3	25.6	0.5
Head width	95.6	33.3	35.6	34.5	0.9
Mouth length	60.3	21.1	23.5	22.2	0.8
Mouth width	81.3	29.5	33.2	30.9	1.0
Barbel length	12.3	2.5	4.4	3.6	0.6
Dentary tooth cup length	32.0	11.5	13.4	12.3	0.7
Premaxillary tooth cup length	27.1	10.4	11.6	11.0	0.3
Occipital length	54.1	17.9	20.0	19.1	0.8
Caudal peduncle length	24.3	24.5	28.2	26.8	1.3
Opercle length	9.7	3.3	5.0	4.0	0.5
Interbranchial distance	25.9	24.2	26.3	24.9	0.7

Table 3. Meristics of *Chaetostoma sacramento*. H = holotype, SD = standard deviation, (n = 11).

Count	H	Min	Max	Mode	SD
Median plates	24	22	24	23	0.5
Supramedian plates	23	22	24	24	0.7
Inframedian plates	24	24	25	24	0.5
Caudal plates rows	5	5	5	5	0.0
Dorsal-fin branched rays	8	8	8	8	0.0
Pectoral-fin branched rays	6	6	6	6	0.0
Pelvic-fin branched rays	5	5	5	5	0.0
Anal-fin branched rays	4	4	4	4	0.0
Caudal–fin branched rays	14	13	14	14	0.3
Dorsal procurrent caudal–fin rays	4	4	4	4	0.0
Ventral procurrent caudal–fin rays	4	2	4	3	0.6
Dorsal fin base plates	7	7	7	7	0.0
Preadipose plates	6	5	5	5	0.0
Adipose-caudal plates	5	6	6	6	0.0
Infraorbital plates	6	6	6	6	0.0
Left dentary teeth	186	82	214	104	40.3
Left premaxillary teeth	115	63	137	86	19.4
Cheek odontodes	4	3	5	5	0.6

Flanks covered by five longitudinal plate series. Plates absent from abdomen and around dorsal-fin base. Body plates flat or gently curved, lacking keel or ridge. Dorsal-fin base bordered laterally by seven dorsal plates. Medial interdorsal plates five. Dorsal plate series with 20 plates, supramedian with 24, median series with 23, mid-ventral series with 24, ventral series with 19.

Dorsal fin II,8; locking mechanism functional, spinelet *V*-shape, dorsal-fin origin slightly anterior to pelvic-fin origin, last dorsal-fin ray not reaching adipose fin when adpressed. Pectoral-fin rays I,6; pectoral-fin spine reaching first third of pelvic fin when adpressed. Pelvic-fin rays i,5; unbranched rays surpassing anal-fin origin; dorsal skin folds present on proximalmost two-thirds of unbranched pelvic-fin rays. Pectoral-fin spine with thicker odontodes irregularly distributed along entire dorsal, anterior and ventral surface of spine; one aligned row of larger odontodes along posterodorsal margin. Odontodes present on all, but posteriormost branched pectoral- and pelvic-fin rays. Anal-fin rays ii,4, first unbranched ray almost as long as second. Second branched anal-fin ray longest, with remaining rays successively shorter. Caudal fin obliquely forked, lower lobe longer than upper; i,7+7,i. Dorsal procurrent caudal-fin rays four, ventral two to four.

Colour in alcohol. Head and body base colour brown dorsally, yellowish-white ventrally. Head with dense small white dots. In some specimens, scattered white spots on the body may be fused. Supraoccipital excrescence black or grey. Dorsal fin with white scattered spots on brownish base composed of melanophores distributed on rays and membrane. Remaining fins with brownish base composed of scattered melanophores. Tip of unbranched dorsal- and caudal-fin rays whitish in some individuals.

Sexual dimorphism. Males with fleshy dorsal fold on the pelvic-fin leading ray. Males have more distinct, intense and contrasting white patterns on darker brown to black base colour. Females with duller colour patterns on lighter brown to black base colour.

Distribution. *Chaetostoma sacramento* is known exclusively from the Pampa de Sacramento valley east of the eastern cordillera of the Andes in Peru, inhabiting the Negro River, a tributary of the Pisqui River in Loreto Department; the Yamino River, a tributary of the Aguaytia River; the Chui River, a tributary of upper San Alejandro River in Ucayali Department; and the Raya River, a left-bank tributary of Iscozacin River in Pasco Department (Fig. 1).

Etymology. The species epithet *sacramento* refers to the plain (pampa) in central Peru between the Huallaga and Ucayali Rivers, approximately delimited by the Pisqui River in the north and Palcazu River in the south. *Chaetostoma sacramento* is currently known exclusively from this region, known as the Pampa de Sacramento, which occupies a valley between Huánuco and Ucayali provinces that is part of the Peruvian subandean belt and surrounds Boqueron del Padre Abad in the Cordillera Azul. The Pampa de Sacramento was first encountered by Europeans on 21 June 1726, by an expedition led by Don Juan Nunez Lobo and was christened Pampa del Sacramento to commemorate the Catholic ceremony of the Corpus Christi. Subsequent Franciscan missionaries highlighted the rich ethnic diversity of this region (IBC 2016). A noun in apposition.

Molecular species delimitation

With 626 total bases and 72 sequences from 12 nominal species, the COI dataset yielded 158 parsimony informative sites (25%). The ASAP species delimitation analysis yielded 20 Molecular Operational Taxonomic units (MOTUs) (score = 2.5), whereas GMYC and bPTP yielded 23 and 22 MOTUs, respectively. These results can be summarised with 22 consensus MOTUs (Fig. 3).

With 1048 total bases and 108 sequences from 24 nominal species, the CytB dataset yielded 355 parsimony informative sites (34%). ASAP (score = 8.0), GMYC and bPTP species delimitation analyses yielded 46, 45, 49 MOTUs, respectively, for a total of 46 consensus MOTUs (Fig. 3).

In all species delimitation analyses of both genes, *Chaetostoma sacramento* was identified as an MOTU distinct from all other examined *Chaetostoma* species. The minimum genetic distance to the nearest species was 6.15% for CytB, with *C. branickii* being the closest species. For COI, the closest species was *C. leucomelas*, with a genetic distance of 4.48%.

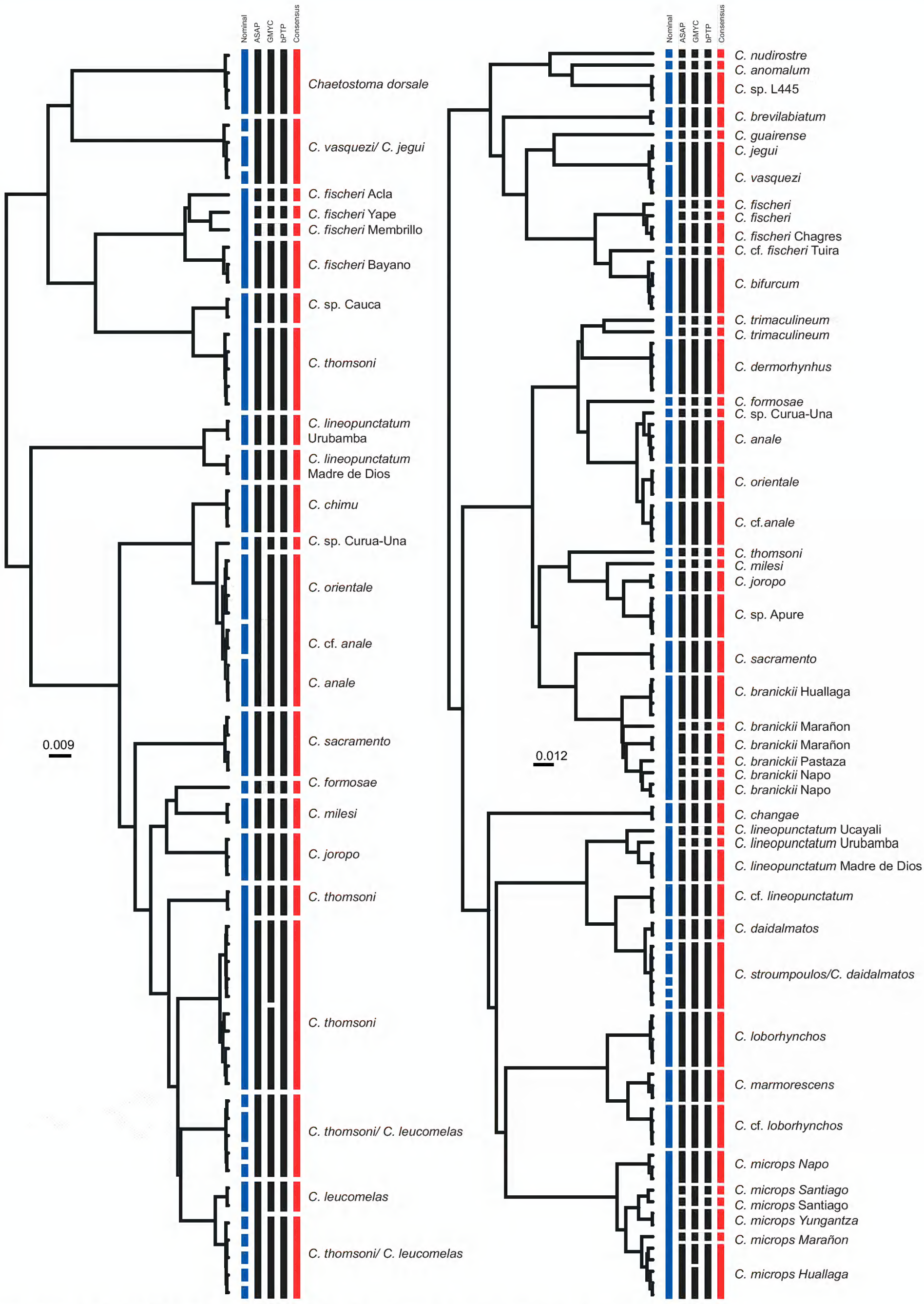

Figure 3. Results of species delimitation analyses, based on COI (left) and CytB (right) gene regions.

Chaetostoma branickii Steindachner 1881

Figs 4, 5

Chaetostoma breve Regan 1904 [synonym]

Diagnosis and description. As for *Chaetostoma breve* in Lujan et al. (2015a).

Comments. Regan (1904) based the description of *Chaetostoma breve* on specimens from the Zamora River in south-eastern Ecuador. Lujan et al. (2015a) re-described *Chaetostoma breve* based on specimens from throughout most of the species' range, from the Napo River in the north (although the species is also now known from more northern Caqueta River headwaters in Colombia; ROM 107831, 107845) to the Marañon River in the south. Lujan et al. (2015a) also generated a multi-locus molecular phylogenetic hypothesis spanning over 24 valid and undescribed species, with *Chaetostoma breve* represented by samples from the Napo, Pastaza, Marañon, Santiago and Huallaga River Basins. Bayesian and Maximum Likelihood analyses found uniformly strong support for monophyly of the entire *Chaetostoma breve* clade (Bayesian posterior probability: 1.00, Maximum Likelihood bootstrap: 100).

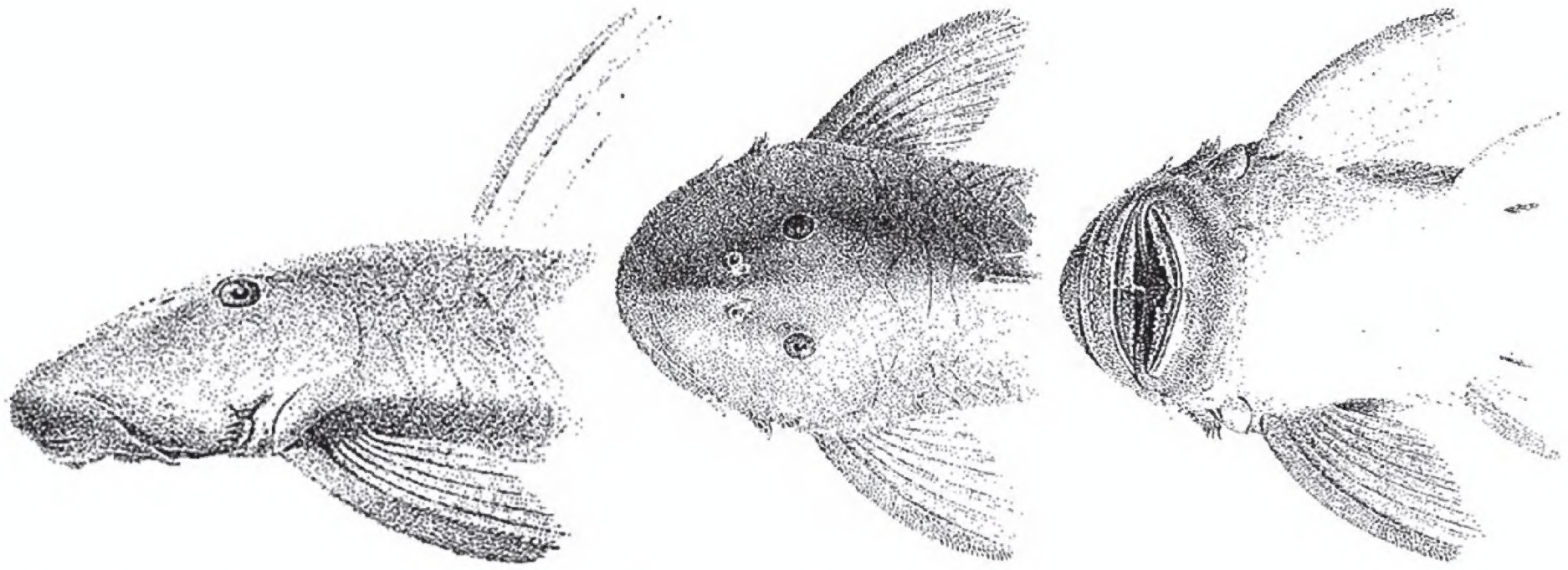

Figure 4. Original illustrations of *Chaetostoma branickii* from Steindachner 1881.

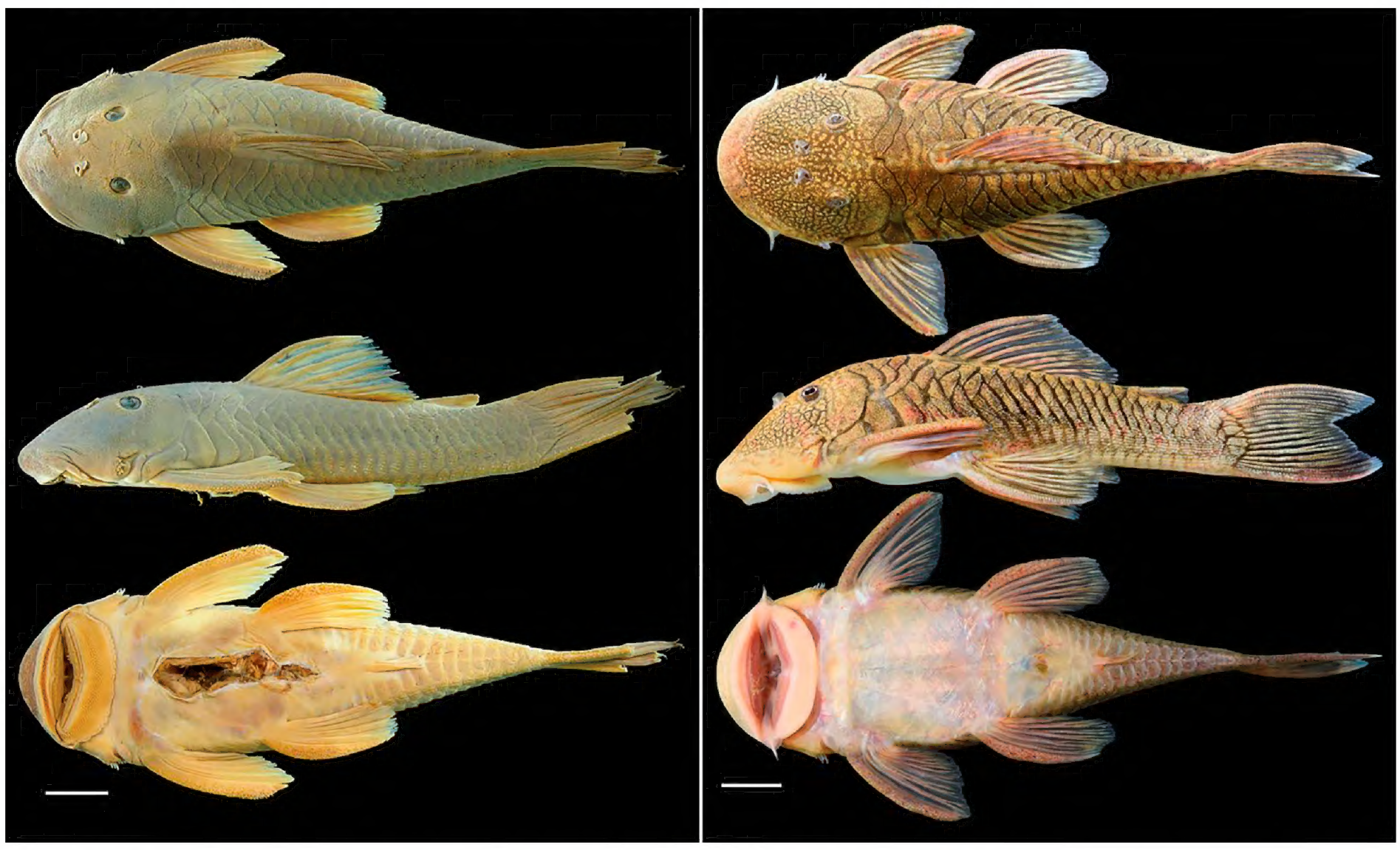

Figure 5. Photo comparison of a nearly 150-year-old preserved syntype of *Chaetostoma branickii* (NMW 47270-71, photos by Mark Sabaj & Kyle Luckenbill, copyright NMW) with a live specimen collected in 2018 from the Marañon River, Cajamarca Province, Peru (ROM 109213, photos by NKL). Scale bars: 1 cm.

Chaetostoma branickii was described by Steindachner (1881), based on specimens from the Chota River near Cajamarca in northern Peru. That portion of the Marañon River Basin was poorly sampled at the time of Lujan et al. (2015c), thus few specimens and no tissues from that specific region were available, making it reasonable to assume that a distinct, endemic species might exist there. Moreover, the syntypes of *Chaetostoma branickii* were in Vienna and not directly accessible to the authors. Lujan et al. (2015c) concluded that *Chaetostoma branickii* might be more closely allied with *Chaetostoma taczanowskii*, which was described by Steindachner (1881), based on specimens from the Huallaga River drainage to the south. To further investigate the validity of *Chaetostoma branickii*, Lujan and colleagues sampled the upper middle Marañon River in 2018, collecting over 540 fresh specimens and 60 tissues of *Chaetostoma*. This new material allowed a more detailed comparison of fresh, nearly topotypic specimens with the specimens on which Lujan et al. (2015a) based their re-description of *Chaetostoma breve* and type images of *Chaetostoma branickii* (Figs 4, 5). Based on this comparison, it has become clear that these are the same species and that *Chaetostoma branickii* should thus be recognised as the senior synonym of *Chaetostoma breve*.

Chaetostoma taczanowskii Steindachner 1882 is another taxonomically ambiguous species from northern Peru, described from the Huallaga River Basin, a southern tributary of the Marañon. Type images of this species suggest that it is also closely related to *Chaetostoma branickii*, if not another junior synonym, but a robust evaluation of the status of this species must await availability of fresh topotypic specimens and tissues.

Discussion

Fourteen *Chaetostoma* species are currently recognised from Peruvian drainages, most of which (12) inhabit the Marañon River Basin, including the Huallaga, Pastaza and Napo Rivers, with only three now described from the Ucayali River Basin: *C. lineopunctatum* from the Pachitea River, *C. loborhynchos* from the Tulumayo Rivers and *C. sacramento*. Until now, the colour pattern described for most species of *Chaetostoma* in Peru comprises black spots on the body and head (*C. daidalmatos*, *C. lineopunctatum*, *C. stroumpoulos*, *C. trimaculineum*) or irregular black spots on the body alone (*C. loborhynchos*, *C. spondylus*). There are also six species described as having uniform or marbled colouration (*C. branickii*, *C. changae*, *C. marmorescens*, *C. lexa* and *C. taczanowskii*). White patterns on a darker base colour are observed in only two species in Peru, *C. dermorhynchus* and *C. microps*, from which *C. sacramento* differs by having distinct and highly variable small to large white spots on the body, head and fins (vs. white spots on only the dorsal fin in C. *dermorhynchus*) and by having eight dorsal-fin branched rays (vs. nine in *C. microps*). Our recognition of *C. sacramento* is further supported by our molecular results, which consistently identify it as a distinct MOTU using the mitochondrial genes COI and CytB. Additionally, our findings demonstrate that *C. dermorhynchus* and *C. microps* each represent a separate MOTU and are phylogenetically distant species to *C. sacramento*, as shown in Lujan et al (2015b).

One of the fundamental criticisms of DNA-based approaches to species delimitation is that such analyses are incapable of distinguishing between genetic structure due to population-level processes and that due to species boundaries (Sukumaran and Knowles 2017). We advocate for a conservative approach in which MOTUs are treated as candidate species to be recognised taxonomically only if they are also morphologically diagnosable. Thus, the combined molecular and morphological evidence supports our recognition of *Chaetostoma sacramento* as a distinct species. Alternatively, the molecular species delimitation analyses consistently subdivided the *Chaetostoma branickii* clade into six MOTUs that we do not recognise as distinct species because of the overall morphologically similarity of these subunits and the strong monophyly of the parent clade. Future research may yet yield morphological characteristics capable of distinguishing these populations, thereby supporting their recognition as distinct species. Such a potentiality would be unlikely to resurrect *Chaetostoma breve*, however, given the very close genetic relationship between individuals from the Santiago (*breve*) and Marañon (*branickii*) river type locality populations, consistent with our decision to recognise *Chaetostoma branickii* as the senior synonym for this species.

Although *Chaetostoma sacramento* has been known in the aquarium fish trade for almost 30 years, it was originally assigned three L-numbers in 2011 (L455, L456 and L457; Seidel (2011)) and is known in the aquarium trade most commonly as L455. Other common aquarium trade names for the species include 'Tiger *Chaetostoma*', 'Tingo Red *Chaetostoma*' or 'Ornate *Chaetostoma*'. Specimens on which the present description is based were collected in the San Carlos River, part of the Palcazu River Basin in Yanachaga Chemillen National Park (PNYC) in 2007 and in the Aguaytia River in 2008. According to aquarium fish exporters, this species also occurs in the Negro River, a small tributary of the upper Pisqui River near the Boqueron del Padre Abad and in the Chiu River, a tributary of San Alejandro River (Seidel 2011).

Acknowledgements

We thank Dario Faustino, Junior Chuctaya, Claudia Nolasco, Omar Quispe, Jerry Arana and Miguel Paniagua for field assistance, Raphael Covain at MHNG for sharing specimens and data and Julian Dignall at PlanetCatfish.com for sharing photos, aquarium literature and his thoughts on L455. This work was financed by CONCYTEC through the PROCIENCIA programme within the framework of the contest "Projects for the incorporation of postdoctoral researchers in Peruvian institutions"

according to contract [074-2021] and [PE501084299-2023-PROCIENCIA-BM] within the framework of the call "Interinstitutional Alliances for Doctorate Programs".

References

Aljanabi SM, Martinez I (1997) Universal and rapid salt-extraction of high-quality genomic DNA for PCR-based techniques. Nucleic acids research 25(22): 4692–4693. https://doi.org/10.1093/nar/25.22.4692

Armbruster JW (2003) *Peckoltia sabaji*, a new species from the Guyana Shield (Siluriformes: Loricariidae). Zootaxa 344: 1–12. https://doi.org/10.11646/zootaxa.344.1.1

Ballen GA, Urbano-Bonilla A, Maldonado-Ocampo JA (2016) Description of a new species of the genus Chaetostoma from the Orinoco River drainage with comments on Chaetostoma milesi Fowler, 1941 (Siluriformes: Loricariidae). Zootaxa 4105(2): 181–197. https://doi.org/10.11646/zootaxa.4105.2.6

Bouckaert R, Heled J, Kühnert D, Vaughan T, Wu CH, Xie D, Suchard M, Rambaut A, Drummond AJ (2014) BEAST 2: a software platform for Bayesian evolutionary analysis. PLoS computational biology 10(4): e1003537. https://doi.org/10.1371/journal.pcbi.1003537

Carvalho TP, Lehmann AP, Reis RE (2008) *Gymnotocinclus anosteos*, a new uniquely-plated genus and species of loricariid catfish (Teleostei: Siluriformes) from the upper rio Tocantins basin, central Brazil. Neotropical Ichthyology 6: 329–338. https://doi.org/10.1590/S1679-62252008000300006

de Queiroz LJ, Cardoso Y, Jacot-des-Combes C, Bahechar IA, Lucena CA, Py-Daniel LR, Soares LM, Nylinder S, Oliveira C, Parente C, Torrente-Vilara G, Covain R, Buckup P, Montoya-Burgos JI (2020) Evolutionary units delimitation and continental multilocus phylogeny of the hyperdiverse catfish genus Hypostomus. Molecular phylogenetics and evolution 145: 106711. https://doi.org/10.1016/j.ympev.2019.106711

Fricke R, Eschmeyer WN, Van der Laan R (2024) Catalog of fishes: genera, species, references. California Academy of Sciences, San Francisco, CA, USA https://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp

Instituto Del Bien Común (IBC) (2016) Estudio previo de reconocimiento de las propuestas de reservas indígenas kakataibo norte y sur. "Proyecto de Regularización de Reservas Indígenas en Aislamiento para la Propuesta de Reserva Indígena Kakataibo".

Larkin MA, Blackshields G, Brown NP, Chenna R, McGettigan PA, McWilliam H, Valentin F, Wallace IM, Wilm A, Lopez R, Thompson JD, Gibson TJ, Higgins DG (2007) Clustal W and Clustal X version 2.0. Bioinformatics 23(21): 2947–2948. https://doi.org/10.1093/bioinformatics/btm404

Lucena CAS, Calegari BB, Pereira EHL, Dallegrave E (2013) O uso de oleo de cravo na eutanasia de peixes. Boletim Sociedade Brasileira de Ictiologia 105: 20–24.

Lujan NK, Armbruster JW, Lovejoy NR, López-Fernández H (2015a) Multilocus molecular phylogeny of the suckermouth armored catfishes (Siluriformes: Loricariidae) with a focus on subfamily Hypostominae. Molecular phylogenetics and evolution 82: 269–288. https://doi.org/10.1016/j.ympev.2014.08.020

Lujan NK, Meza-Vargas V, Astudillo-Clavijo V, Barriga-Salazar R, López-Fernández H (2015b) A multilocus molecular phylogeny for *Chaetostoma* clade genera and species with a review of *Chaetostoma* (Siluriformes: Loricariidae) from the Central Andes. Copeia 103: 664–701. https://doi.org/10.1643/CI-14-194

Lujan NK, Meza-Vargas V, Barriga-Salazar R (2015c) Two new *Chaetostoma* group (Loricariidae: Hypostominae) sister genera from opposite sides of the Andes Mountains in Ecuador, with the description of one new species. Copeia 103(3): 651–663. https://doi.org/10.1643/CI-15-246

Meza-Vargas V, Calegari BB, Lujan NK, Ballen GA, Oyakawa OT, Sousa LM, Reis RE (2022) A New Species of *Chaetostoma* (Siluriformes: Loricariidae) Expands the Distribution of Rubbernose Plecos Eastward into the Lower Amazon Basin of Brazil. Ichthyology & Herpetology 110(2): 364–377. https://doi.org/10.1643/i2021068

Neuhaus EB, Meza-Vargas V, Herrera JR, Lujan NK (2023) A new distinctively striped species of bushynose catfish (Siluriformes: Loricariidae: *Ancistrus*) from the Pachitea River drainage, Pasco, Peru. Journal of Fish Biology 104(4): 969–978. https://doi.org/10.1111/jfb.15637

Pons J, Barraclough TG, Gomez-Zurita J, Cardoso A, Duran DP, Hazell S, Kamoun S, Sumlin WD, Vogler AP (2006) Sequence-based species delimitation for the DNA taxonomy of undescribed insects. Systematic biology 55(4): 595–609. https://doi.org/10.1080/10635150600852011

Puillandre N, Brouillet S, Achaz G (2021) ASAP: assemble species by automatic partitioning. Molecular Ecology Resources 21(2): 609–620. https://doi.org/10.1111/1755-0998.13281

Rambaut A, Suchard MA, Xie D, Drummond AJ (2014) Tracer v1. 6.

Ramirez JL, Galetti Jr PM (2015) DNA barcode and evolutionary relationship within *Laemolyta* Cope 1872 (Characiformes: Anostomidae) through molecular analyses. Molecular Phylogenetics and Evolution 93: 77–82. https://doi.org/10.1016/j.ympev.2015.07.021

Ramirez JL, Valdivia P, Rosas-Puchuri U, Valdivia NL (2023) SPdel: A pipeline to compare and visualize species delimitation methods for single-locus datasets. Molecular Ecology Resources 23(8): 1959–1965. https://doi.org/10.1111/1755-0998.13864

Regan CT (1904) "A monograph of the fishes of the family Loricariidae." Transactions of the Zoological Society of London 17: 191–350. https://doi.org/10.1111/j.1096-3642.1904.tb00040.x

Sabaj MH (2020) Codes for natural history collections in ichthyology and herpetology. Copeia 108(3): 593–669. https://doi.org/10.1643/ASIHCODONS2020

Salcedo NJ, Ortega H (2015) A new species of *Chaetostoma*, an armored catfish (Siluriformes: Loricariidae), from the río Marañón drainage, Amazon basin, Peru. Neotropical Ichthyology 13(1): 151–156. https://doi.org/10.1590/1982-0224-20140073

Salcedo NJ (2006a) New species of *Chaetostoma* (Siluriformes: Loricariidae) from Central Peru. Copeia 2006(1): 60–67. https://doi.org/10.1643/0045-8511(2006)006[0060:NSOCSL]2.0.CO;2

Salcedo NJ (2006b) Two new species of *Chaetostoma* (Siluriformes: Loricariidae) from the Huallaga River in central Peru. Ichthyological Exploration of Freshwaters 17(3): 207–220. https://doi.org/10.1643/0045-8511(2006)006[0060:NSOCSL]2.0.CO;2

Schaefer SA (1997) The neotropical cascudinhos: systematics and biogeography of the *Otocinclus* catfishes (Siluriformes: Loricariidae). Proceedings of the Academy of Natural Sciences of Philadelphia 148: 1–120.

Seidel I (2011) Gleich drei neue *Chaetostoma*-Arten aus Peru. Neu importiert 2011: 28–29.

Stawikowski R (1988) "Harnischwelse aus südlichen Amazonaszuflüssen." Die Aquarien- und Terrarienzeitschrift (DATZ) 41: 556–558.

Steindachner F (1881) "Beiträge zur Kenntniss der Flussfische Südamerika's. II." Denkschriften der Mathematisch-Naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften in Wien 43: 103–146.

Sukumaran J, Knowles L (2017) Multispecies coalescent delimits structure, not species. Proceedings of the National Academy of Sciences 114:1607–1612. https://doi.org/10.1073/pnas.1607921114

Zhang J, Kapli P, Pavlidis P, Stamatakis A (2013) A general species delimitation method with applications to phylogenetic placements. Bioinformatics 29(22): 2869–2876. https://doi.org/10.1093/bioinformatics/btt499